Trees (2011) 25:115–124
DOI 10.1007/s00468-010-0478-x

ORIGINAL PAPER

Assessing long-term changes in tropical forest dynamics: a first test using tree-ring analysis

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Received: 15 December 2009 / Revised: 23 April 2010 / Accepted: 28 July 2010 / Published online: 10 August 2010

Abstract There is growing evidence that tree turnover in tropical forests has increased over the last decades in permanent sample plots. This phenomenon is generally attributed to the increase in atmospheric CO_2, but other causes cannot be ruled out. A proper evaluation of historical shifts in tree turnover requires data over longer periods than used so far. Here, we propose two methods to use tree-ring data for detecting long-term changes in tree turnover. We apply these methods to two non-pioneer tree species in a Bolivian moist forest. First, we checked for temporal changes in the frequency of growth releases to determine whether this frequency has increased over time. Second, we calculated the degree of temporal autocorrelation—a measure that indicates temporal changes in growth rates that are likely related to canopy dynamics—and checked for changes in this parameter over time. In addition, we performed analyses that corrected for ontogenetic increases in the measures used by analyzing residuals from size–growth relations. No evidence for the occurrence of a large-scale disturbance was found as we did not observe synchronization in the occurrence of releases in time. For both species, we did not detect changes in autocorrelation or release frequency over the last 200–300 years. Only in one size category, we found increased release frequency over time, probably as a result of a remaining ontogenetic effect. In all, our analyses do not provide evidence for long-term changes in tree turnover in the study area. We discuss the suitability of the proposed methods.

Keywords Forest dynamics · Growth release · Autocorrelated growth · Ontogeny · Tree turnover · Bolivia

Communicated by A. Bräuning.

Contribution to the special issue "Tropical Dendroecology".

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Introduction

There is a growing amount of evidence that tropical forests are changing. Growth rates of individual trees increased over the last decades in permanent sample plots (Laurance et al. 2004; Phillips et al. 2008) as did aboveground biomass (Baker et al. 2004) and tree turnover (Phillips and Gentry 1994; Lewis et al. 2004b; Phillips et al. 2004; Laurance et al. 2009). These changes have been attributed to climate change, in particular to the increase in atmospheric CO_2 (Lewis et al. 2004a). Elevated levels of CO_2 may have increased rates of photosynthesis and as a result stimulated tree growth. At stand level, such changes may have increased rates of growth, recruitment, and mortality, resulting in a higher stem density and increased aboveground biomass (Lewis et al. 2004a; Phillips et al. 2008). An alternative explanation for the observed change in tropical forest biomass is the occurrence of historical (large scale) disturbances (Chave et al. 2008). If forests are

recovering from such disturbances, an increase in biomass over time is observed.

Although the evidence for increased biomass and tree turnover in tropical forests is now quite strong, the causes of these increases are widely and intensively debated (e.g. Wright 2005; Lewis et al. 2004a, 2006). Methodological problems have been proposed as causes, including sampling biases related to the size, amount, and location of the permanent forest plots, which may have led to observing increases in biomass (Feeley et al. 2007; Chave et al. 2008; Fisher et al. 2008). Similarly, the varying intervals between re-measurements of the plots have been suggested to result in an increase in tree turnover (Sheil 1995). To account for the latter bias, corrections have been applied (cf. Lewis et al. 2004b, c; Phillips et al. 2004). No evidence was found for a sampling bias due to intrinsic temporal patterns of forest biomass growth and decline (Gloor et al. 2009).

So far, temporal patterns in forest dynamics have been evaluated over relatively short time periods, spanning just the last few decades (e.g. Phillips et al. 2004). Atmospheric CO_2, however, has increased over the last 150 years (IPCC 2007). Moreover, any recovery from past disturbances is a long-term process that would take many decades. Thus, to study these effects, long-term data are required. One option to obtain such data is the application of tree-ring analysis (Rozendaal and Zuidema 2010). Tree-ring analysis has been successfully used to show that diameter growth of four Bolivian tree species has gradually increased over the last centuries (Rozendaal et al. 2010). In order to detect changes in tree turnover, it is necessary to analyze the temporal variation in tree-ring width instead of the average or median values. An increase in tree turnover over time implies an increase in the frequency of canopy gap formation. The formation of canopy gaps back in time can be reconstructed using tree-ring analysis, as growth rates of the remaining trees temporarily increase when a gap is formed. These growth releases can be found in tree-ring data as periods of a sudden increase in growth, which is sustained over time (Nowacki and Abrams 1997). Thus, an increase in the frequency of occurrence of releases over time may indicate an increase in tree turnover. Tree-ring analysis has been widely applied to reconstruct the disturbance history of temperate forests (e.g. Runkle 1982; Lorimer and Frelich 1989; Lusk and Smith 1998) and recently also in the tropics for a seasonally dry forest in Thailand (Baker et al. 2005).

Another way of evaluating whether tree growth patterns have changed over time considers the temporal patterns in growth autocorrelation. Tree growth tends to be autocorrelated in time (e.g. Kohyama and Hara 1989; Kammesheidt et al. 2003; Grogan and Landis 2009), i.e. the growth of a tree in 1 year is correlated with that in the subsequent year. Such growth autocorrelation of individual trees—'within-tree autocorrelation'—has been found to be strong for a number of tropical tree species (Brienen et al. 2006). Within-tree autocorrelation has been suggested to increase when a tree switches more often between periods of slow and fast growth (Brienen et al. 2006). As the occurrence of periods of suppression and release in growth are associated with gap dynamics, we expect within-tree autocorrelation to increase with increasing tree turnover.

In this study, we evaluate the suitability of these two methods—detection of releases and analysis of autocorrelation—to assess evidence for long-term changes in tropical forest dynamics. The following research questions were addressed: (1) Has the frequency of occurrence of releases changed over time? (2) Has the strength of within-tree autocorrelation increased over time?

We applied these methods to two Bolivian non-pioneer tree species using long-term growth data from tree-ring measurements. Trees over the entire diameter range of the species were sampled to evaluate changes in within-tree autocorrelation and frequency of growth releases over the last 2–3 centuries.

Materials and methods

Study area and species

Fieldwork was conducted in a semi-deciduous moist forest area, 'Los Indios' (10°26′S, 65°33′W), in the department of Pando, Bolivia. Mean annual precipitation is 1,660 mm (Riberalta), with a dry season (<100 mm per month) from May until September. The forest has an average canopy height of 33 m and stem density of 423 stems ha^{-1} (of stems >10 cm diameter at breast height (dbh; Toledo et al. 2008). Fieldwork was conducted in 2006 and 2007, just after selective logging (2–3 trees ha^{-1}) had taken place. Before that, the forest was not harvested, and no evidence for large-scale historical disturbances exists. Two shade-tolerant canopy tree species were included: *Clarisia racemosa* Ruíz & Pavón and *Peltogyne* cf. *heterophylla* M.F. Silva, which will be further referred to by their generic name only. Both species form annual rings in both the juvenile and the adult stage (Soliz-Gamboa et al. 2010). Fieldwork for *Clarisia* was done in an area of ~400 ha and for *Peltogyne* in an area of ~170 ha. Research areas for the two species did not overlap.

Sample collection and ring width measurements

We randomly selected 57 and 62 trees of <50 cm dbh and 30 and 29 trees of >50 cm dbh for *Clarisia* and *Peltogyne*, respectively (cf. Rozendaal et al. 2010). We selected individuals of <50 cm dbh such that they were evenly

distributed over diameter categories. In order to reduce spatial autocorrelation in growth rates, selected individuals needed to be at least 20 m apart. Damaged juveniles (<10 cm dbh) were not included.

Disks were obtained from the selected individuals at 0.5 m height for *Clarisia* and at 1 m height for *Peltogyne*. In the case of trees >50 cm dbh, we always collected disks from stumps of logged trees. A digital picture of each disk was taken to calculate fresh disk area using pixel-counting software (SigmaScan Pro 5.0). Disks were air-dried and sanded with progressively finer sandpaper until a grit of 1,000. Rings were marked in three or four radii—selected to correspond to total disk area—using a stereomicroscope (6.3–40×). Every tenth ring was connected over the whole disk to control for errors in ring identification. Ring widths were measured perpendicular to the ring boundaries using a LINTAB 5 (Rinntech) measurement device. The last formed ring (2006, growth period 2006–2007) was left out for the trees >50 cm dbh as this ring was formed after selective logging. Ring widths of all radii of the disks were averaged, corrected for desiccation and irregular growth using the mean radius of the fresh disk area. Part of the samples could be cross-dated and were used to build chronologies (Soliz-Gamboa et al. 2010). For both species, significant correlations with rainfall were found. Many samples were not included in the chronologies, which could mean that there may be some dating errors remaining (Soliz-Gamboa et al. 2010). Still, for the analyses we performed in this study, we do not expect these inaccuracies to have influenced the results.

Calculating and analyzing growth releases

Relative changes in diameter growth were calculated. A moving average of 10 years was applied to remove long-term age-effects and short-term climatic fluctuations. Percent growth change was calculated following the approach of Nowacki and Abrams (1997):

$$\%\mathrm{GC}_i = [(M_2 - M_1)/M_1] \times 100, \quad (1)$$

where $\%\mathrm{GC}_i$ = percentage growth change between the preceding and subsequent 10-year means of year i, M_1 = mean diameter growth over the preceding 10 years (including year i), and M_2 = mean diameter growth over the subsequent 10 years. A period with $\%\mathrm{GC} > 50\%$, which lasted for at least 10 years was regarded as a release. However, growth rates increase with tree size (e.g. Clark and Clark 1999). If this ontogenetic increase in growth is strong, in spite of the application of a moving average, it may result in a high %GC and even lead to the detection of a release (cf. Fig. 1a). To correct for this size-related effect, we determined residual growth: the residuals of a species-specific linear regression between average size (for trees up to 20 cm diameter) and growth (Fig. 1b). These residuals were used to calculate growth changes, corrected for the ontogenetic increase in growth. We

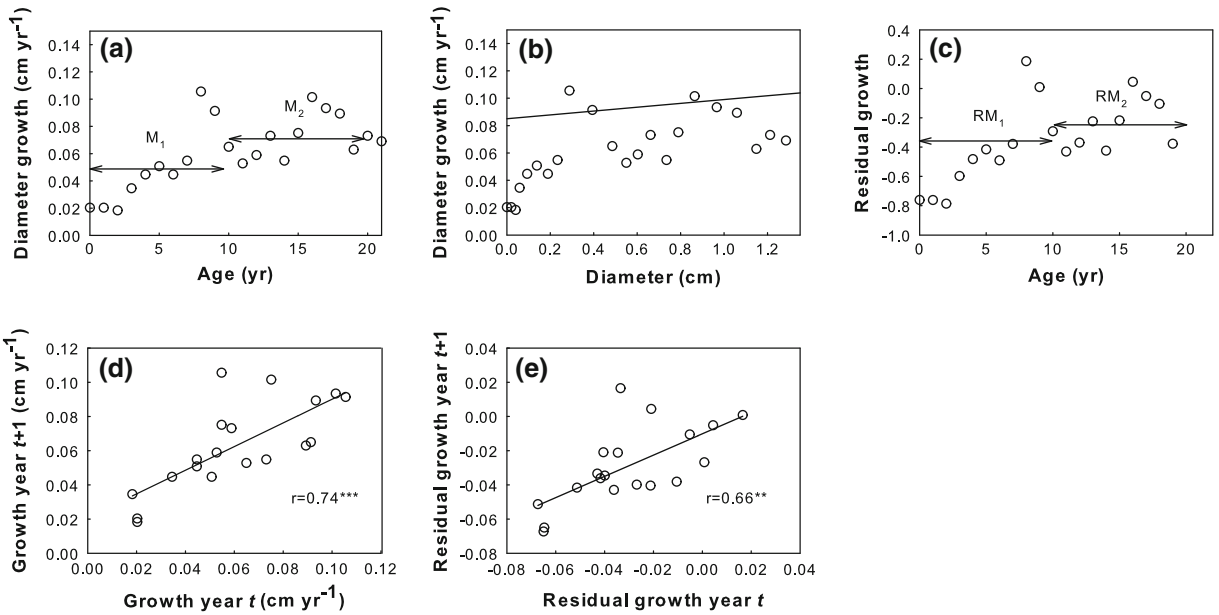

Fig. 1 Example of growth patterns of a *Clarisia* tree. **a** Diameter growth over the first 20 years (initial diameter is 0 cm) of the lifespan of an individual tree. Moving averages M_1 and M_2 are indicated. **b** Relation between size and diameter growth. The *line* represents the average relation between size and growth rate for *Clarisia*. **c** Residuals from the average relation between tree size and growth rate in proportion to the average relation between tree size and growth rate. Moving averages are indicated. **d** Within-tree autocorrelation for the initial diameter of 0 cm. **e** Autocorrelation in the residuals for the initial diameter of 0 cm

expressed the residuals in proportion to the average relation between size and growth. Then we calculated a measure similar to the percentage change of growth residuals (residual growth change; $\%RGC_i$; cf. Fig. 1c):

$$\%RGC_i = (MR_2 - MR_1) \times 100, \quad (2)$$

where $\%RGC_i$ = percentage change in growth residuals between the preceding and subsequent 10-year averages, MR_1 = mean residual diameter growth over the preceding 10 years (including year i), and MR_2 = mean residual diameter growth over the subsequent 10 years. A period with $\%RGC > 50\%$, which lasted for at least 10 years was regarded as a release. Note that here growth of each year is standardized for the relation between average size and growth rate. The difference between MR_1 and MR_2 is not expressed in proportion to MR_1, but in proportion to the average relation between size and growth rate. We chose to use this approach, instead of the boundary-line method for detecting releases (Black and Abrams 2003), as that method does not fully correct for tree size and requires a large amount of points to establish the boundary line (Black et al. 2009).

First, we evaluated whether there was evidence for the occurrence of a large-scale disturbance in the study area (cf. Baker et al. 2005). To do so, the dataset was divided into 25-year periods, among which the percentage of trees with a release starting in each time period was compared. Second, the occurrence of releases in growth was related to time. To allow comparison of the occurrence of releases and strength of autocorrelation among trees at the same diameter, and thus in the same ontogenetic stage, we expressed all variables for a timespan of 20 years starting at different tree diameters (i.e. initial diameter 0, 2.5, 5, 10, 15, and 20 cm) per individual tree. Presence or absence of a release was scored for the same 20 years. For each individual and each initial diameter, we also calculated the mid-point of the ages of those 20 years, which we termed year before present (YBP; the time axis, cf. Rozendaal et al. 2010). The calendar year for the 'present year' in the calculation of YBP was 2006, the year of data collection. A logistic regression was performed to relate the presence or absence of a release to YBP for each initial diameter.

Calculating within-tree autocorrelation

Within-tree autocorrelation was calculated as the correlation of growth of an individual tree in a certain year t with its growth in the subsequent year $t + 1$ using Pearson's correlation. We expressed autocorrelation in time periods of 20 years starting at the same initial diameters as for the frequency of releases. In this way, the comparison of the strength of autocorrelation among trees was facilitated. Additionally, we calculated strength of autocorrelation corrected for tree size. A fast-growing individual tree passes in 20 years through a larger diameter range than a slow-growing tree, which could mean that in those 20 years a fast-growing tree has a larger ontogenetic increase in growth rate, and thus, stronger within-tree autocorrelation. Autocorrelation was calculated from the residuals of a linear regression between size and average growth rates up to 20 cm diameter. Then strength of autocorrelation was related to YBP using a mixed modeling approach as data points were not independent due to the inclusion of multiple values per tree (one value per initial diameter). Initial diameter was included as a factor and YBP as a covariate. To analyze the influence of ontogeny, we also included the mean diameter growth rate over the same 20-year period as a covariate. This approach was applied for within-tree autocorrelation and the autocorrelation in the residuals. All statistical analyses were performed using SPSS 16.0 (SPSS Inc.).

Results

Size-dependent growth rates, growth releases, and autocorrelation

Growth rates strongly increased with tree size for both species (Fig. 2). In *Clarisia*, average growth rate at 0 cm

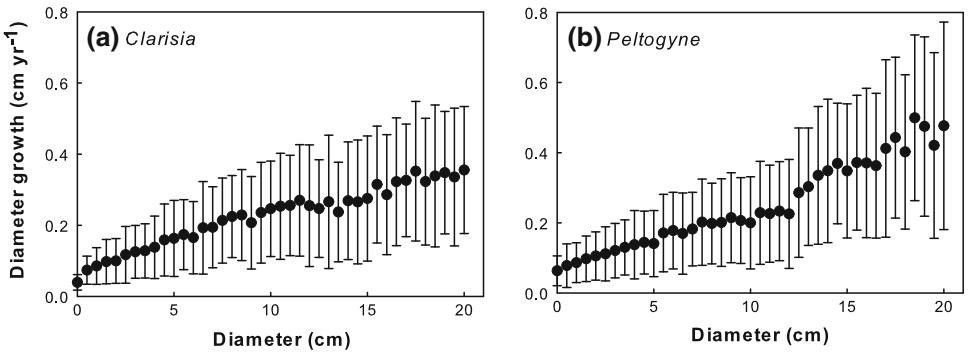

Fig. 2 Average relation between tree diameter and diameter growth for two tropical tree species. *Error bars* are standard deviations

diameter, 0.04 cm year^{-1}, showed a ninefold increase to 0.36 cm year^{-1} at 20 cm diameter. For *Peltogyne*, this initial increase was also strong, eightfold, from 0.06 cm year^{-1} at 0 cm diameter to 0.48 cm year^{-1} at 20 cm diameter. This increase is probably due to larger leaf area available for assimilation and to some extent an increase in light with increasing tree height.

The occurrence of releases showed a strong pattern with tree size and differed between species (Fig. 3a). *Clarisia* showed more releases at the initial diameters of 0, 2.5, and 5 cm. A lower percentage of trees experienced a release at larger diameters. For *Peltogyne*, the opposite pattern was found as releases mostly occurred at the initial diameters of 10 and 15 cm (Fig. 3a). *Clarisia* showed strong within-tree autocorrelation in the 20-year period starting at 0 cm diameter; autocorrelation was lower for the larger initial diameters (Fig. 3c). For *Peltogyne*, autocorrelation was low in the time period starting at 2.5 cm diameter. Hence, for this species, autocorrelation does not seem to increase or decrease with increasing tree size. The strong autocorrelation at small size for *Clarisia* may be a consequence of the relatively steep increase in growth from 0 to 2.5 cm diameter compared to the increase at larger diameters (cf. Fig. 2). In contrast, *Peltogyne* showed a less steep increase until ~12.5 cm diameter, but a steeper increase from 12.5 cm onwards (Fig. 2b).

Assessing changes in release frequency over time

To evaluate the degree of synchronization in time in the occurrence of releases, we compared the occurrence of releases in 25-year periods. In general, there was no clear pattern in the occurrence of releases for both species, but the percentage of trees with a release varied somewhat over the past 200–300 years (Fig. 4). As *Clarisia* reaches a higher age than *Peltogyne*, there were >10 trees present in the sample from 1,700 onwards, while for *Peltogyne* this was from 1,825 onwards. We found releases in all time intervals for both species and did not detect a clear clustering of releases at any moment in time in the past centuries (Fig. 4).

To determine whether recently the occurrence of releases increased over time, we related the presence or absence of a release to year before present (YBP) with a logistic regression for each initial diameter. At most initial diameters, we did not find a relation between the occurrence of releases and YBP (Fig. 5). For both species, we found a significant increase in releases over time in the 20-year interval at an initial diameter of 0 cm and for *Peltogyne* also at 2.5 cm diameter (Fig. 5). This may be partially due to the structure of the dataset as sample sizes are largest at small tree size. At those sizes, both juvenile growth rates of large trees and growth rates of extant juvenile trees are included. Additionally, the range in YBP is largest at small tree sizes as growth rates of the oldest and youngest trees are included.

When evaluating the occurrence of releases corrected for growth releases caused by the ontogenetic pattern in growth, much less releases were detected for both species (Fig. 3b). However, at an initial diameter of 0 cm, an increase in the occurrence of releases over time was still

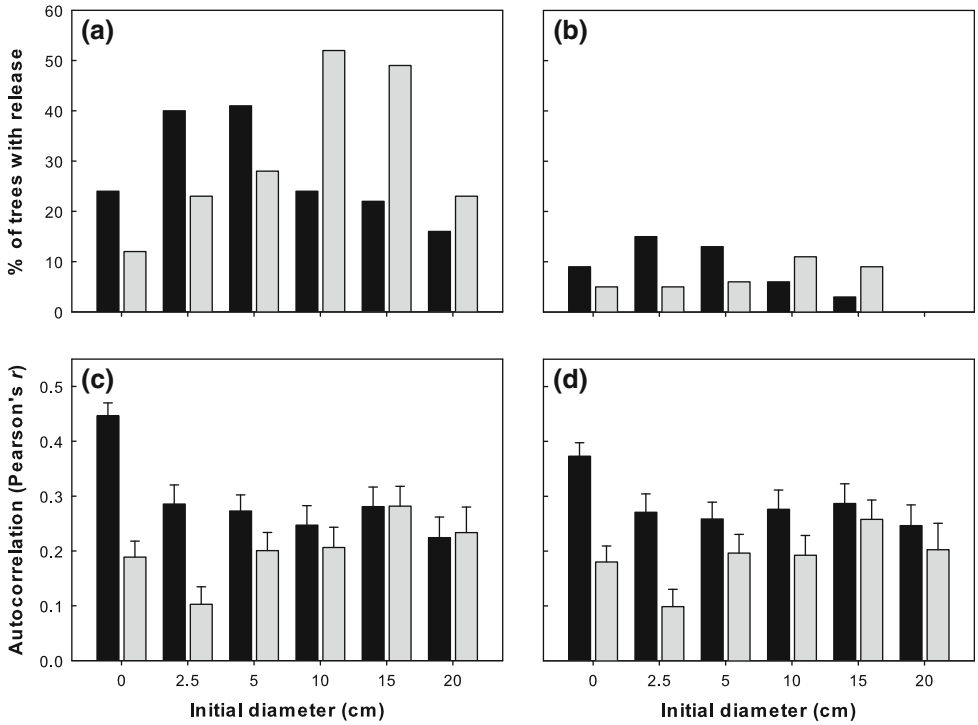

Fig. 3 Average within-tree autocorrelation with standard error and percentage of trees with a release in a 20-year time period starting at different initial diameters. *Black bars* indicate values for *Clarisia*; *gray bars* represent values for *Peltogyne*. **a** Percentage of trees with a release. **b** Percentage of trees with a release after correction for the relation between size and growth rate. **c** Within-tree autocorrelation. **d** Within-tree autocorrelation in residuals from a regression between tree size and growth rate

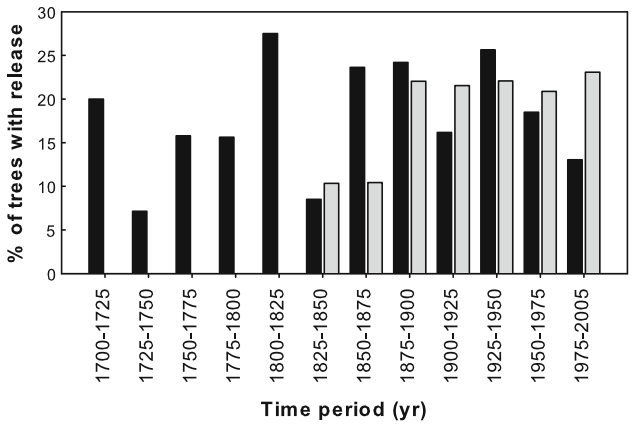

Fig. 4 Percentage of trees with a release in 25-year time periods for *Clarisia* (*black bars*) and *Peltogyne* (*gray bars*). Percentages were only indicated for time periods with at least ten trees present

observed for *Clarisia*, as well as for *Peltogyne*. Nevertheless, the number of trees with a release was very low, eight for *Clarisia* and only five for *Peltogyne* (cf. Fig. 3b).

Changes in autocorrelation over time

Temporal patterns in the strength of autocorrelation were evaluated using a mixed modeling approach. For *Clarisia*, a significant negative relation between within-tree autocorrelation and YBP was observed, which indicates an increase in within-tree autocorrelation over time (Table 1; Fig. 6). In *Peltogyne*, we found no relation between within-tree autocorrelation and YBP (Table 1; Fig. 6). Within-tree autocorrelation did not vary with tree size in *Clarisia*, whereas for *Peltogyne* within-tree autocorrelation differed among initial diameters and increased with average diameter growth rate (Table 1).

When correcting for the relation between tree size and growth rate, autocorrelation was somewhat lower in *Clarisia* at an initial diameter of 0 cm (Fig. 3d). When using autocorrelation in growth residuals, no significant effect of YBP was found for any of the species (Table 1). For *Peltogyne*, a positive relation between average growth rate and within-tree autocorrelation was still found, even when using residual growth (Table 1). Similarly, there was still an effect of initial diameter on within-tree autocorrelation for *Peltogyne*.

Discussion

Ontogeny and the occurrence of releases and within-tree autocorrelation

Tree growth is known to increase with tree size (e.g. Clark and Clark 1999). With increasing tree size, trees have larger leaf area available for assimilation. Additionally, growth rates are known to increase with increasing tree height (Claveau et al. 2002), probably as a consequence of the increase in light availability with increasing tree height (cf. Sterck et al. 2001). An ontogenetic growth increase may lead to the detection of a release. If the ontogenetic increase is strong, the difference between the averages of the preceding 10 years may differ strongly from that of the subsequent 10 years and result as such in a large growth change. This may be the case for *Clarisia* in particular as in this species the initial increase in growth with tree size is relatively steep (cf. Fig. 2). Similarly, the larger number of releases for *Peltogyne* at the initial diameters of 10 and 15 cm may be the consequence of the steeper ontogenetic increase in growth at those tree sizes. The detection of a much lower number of releases after correcting for size-related growth confirms this idea.

An ontogenetic growth increase may cause strong autocorrelated growth. Brienen et al. (2006) attributed the stronger autocorrelation for trees <10 cm dbh to the frequent alternation of suppressions and releases at that tree size. However, they also show that the use of residual growth results in lower within-tree autocorrelation although the decrease differed among species (Brienen et al. 2006). Our results show that accounting for the relation between size and growth did not result in a large reduction in within-tree autocorrelation. After correcting for the average relation between size and growth, autocorrelation still increased with growth rate in *Peltogyne* (Table 1). This may be due to the fact that we calculated residuals based on an average relation between size and growth rate, rather than the observed relation for *individual* trees. Thus, differences among fast- and slow-growing trees at the same tree size were still present in the dataset of residuals and may be largely responsible for the strong autocorrelation that we observed.

Evidence for changing forest dynamics over time?

Two methods were proposed to assess changes in forest dynamics over time using tree-ring analysis: the occurrence of releases and the strength of within-tree autocorrelation. In addition to that, we evaluated synchrony in the occurrence of releases over time to identify possible large disturbances. Although some variation in the occurrence of releases over time was observed, evidence for a large-scale disturbance was not found. At small tree diameters, we observed an increase in the frequency of releases over time in both species and an increase in within-tree autocorrelation over time for *Clarisia*. However, these patterns were likely caused by an ontogenetic increase in growth. When accounting for an ontogenetic increase in growth, neither temporal changes in within-tree autocorrelation, nor

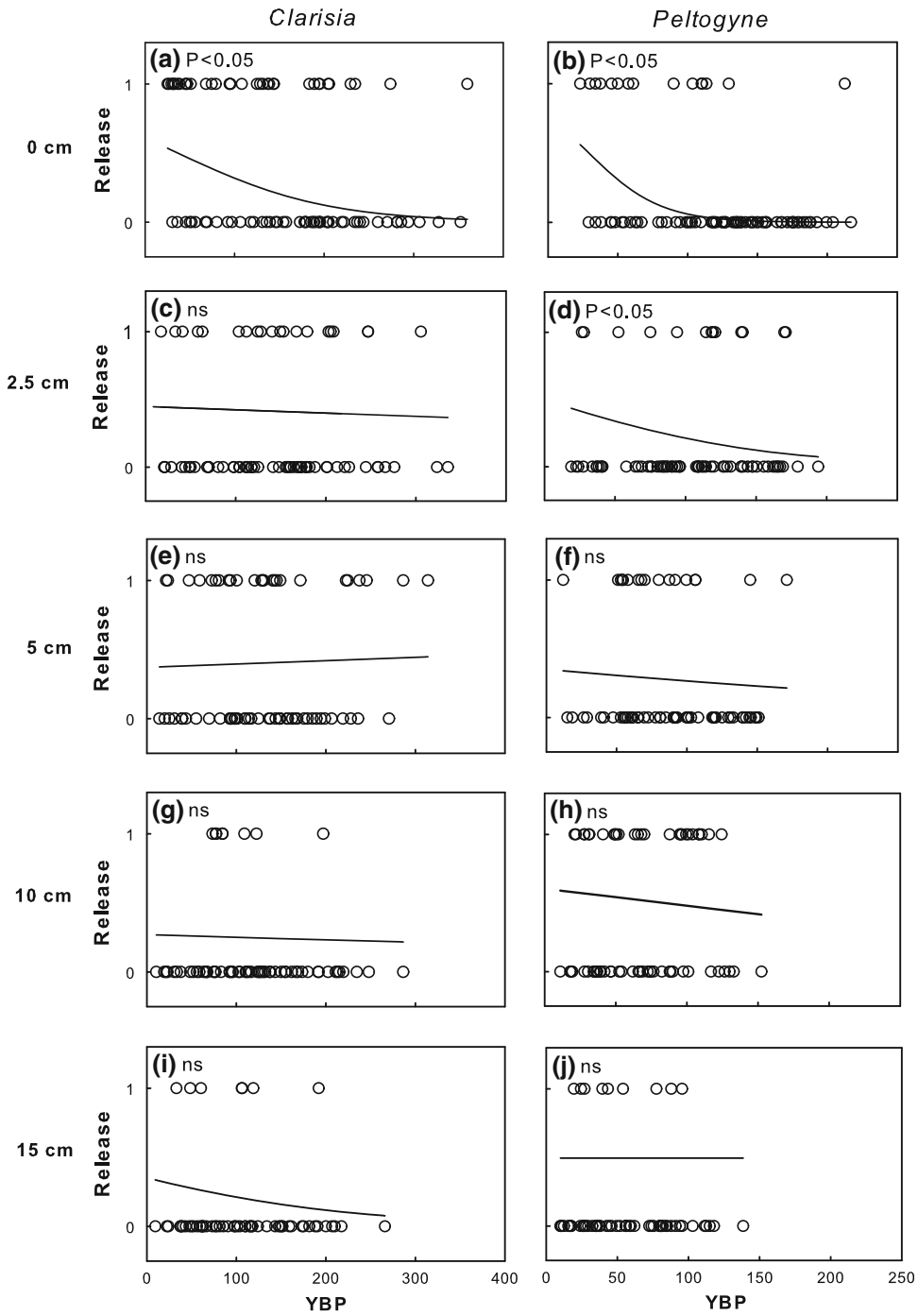

Fig. 5 The occurrence of releases (based on ring widths, not on residual growth) related to the number of years before present (YBP; year before 2006) for two tropical tree species at different tree sizes

reliable temporal changes in the occurrence of releases were found. At an initial diameter of 0 cm, still a temporal change in the occurrence of releases was found for both species, but only very few trees showed a release (cf. Fig. 3b). Thus, the results should be interpreted cautiously. We did not find evidence for a change in forest dynamics over time in the study area, but the lack of patterns may be partly, or entirely, due to methodological constraints. Changes in forest dynamics may have occurred, but we might not have been able to detect those.

Future directions

The application of tree-ring analysis may be a promising tool in evaluating temporal patterns in tropical forest dynamics. However, causes of growth releases and within-tree autocorrelation should be unraveled further to develop more suitable methods to detect light-related growth changes. It may be more appropriate to define criteria to detect releases specifically for tree species and forest types (cf. Rubino and McCarthy 2004). Baker and Bunyavejchewin

Table 1 Results of a mixed model analysis to determine the effects of initial diameter (tree size) on autocorrelation and on autocorrelation in the residuals from the relation between tree size and growth in a 20-year period

	Clarisia				*Peltogyne*			
	Autocorrelation		Residuals		Autocorrelation		Residuals	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Initial diameter	0.507	0.771	0.881	0.494	**2.430**	**0.035**	**3.064**	**0.010**
YBP	**4.032**	**0.045**	2.855	0.092	0.006	0.941	0.018	0.894
DGR	0.000	0.985	0.118	0.732	**12.622**	**0.000**	**8.696**	**0.003**
Initial diameter × YBP	0.369	0.870	0.409	0.842	1.049	0.388	0.886	0.491
Initial diameter × DGR	1.733	0.126	1.840	0.104	**3.494**	**0.004**	**3.801**	**0.002**
YBP × DGR	**3.885**	**0.049**	2.714	0.100	0.369	0.544	0.136	0.713

Year before present (YBP; year before 2006) and average diameter growth for the same 20 years were included as covariates. Bold values indicate significant effects at $P < 0.05$

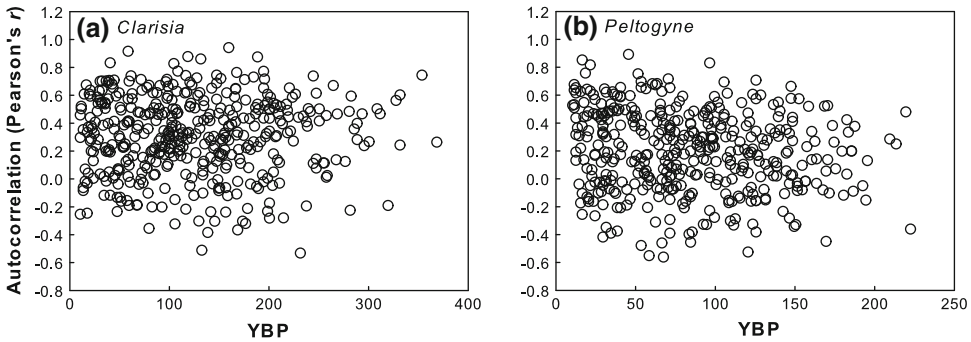

Fig. 6 Relation between within-tree autocorrelation for a 20-year timespan and average year before present (YBP; year before 2006). Values for all tree sizes are shown based on ring widths instead of residual growth

(2006), for instance, defined releases based on threshold values in observed light levels and also in temperate forests releases have been defined in a similar way (e.g. Lorimer et al. 1988). Another way of defining releases is a direct comparison of growth before and after canopy gap formation for the same tree, which has been done for temperate tree species in silvicultural studies about thinning treatments (cf. Bebber et al. 2004; Bevilacqua et al. 2005), and for a few tree species in tropical forest after selective logging took place (Soliz-Gamboa 2010). Such direct measurements of growth responses to disturbances may be used to calibrate release-and-suppression patterns in tree-ring series. Such calibration increases the chance that observed growth releases were indeed triggered by improved light conditions.

It should be taken into account that we worked on a rather coarse spatial scale as we included, on average, less than one tree per 2 ha (*Peltogyne*) or per 4 ha (*Clarisia*). To capture all variation in canopy dynamics and to be able to define forest turnover (e.g. Hartshorn 1978) or that proportion of the forest canopy that is annually opened through gap formation (e.g. van der Meer and Bongers 1996), gap dynamics should also be evaluated on smaller spatial scales. A possible sampling design may be the inclusion of various clusters of trees, with the clusters distributed over a larger area. In this way, changes at different spatial scales can be detected (cf. Baker et al. 2005). Additionally, our sample size was small. To determine changes in forest structure in a single area, a sample of at least 1,000 trees has been suggested to be sufficient (cf. Hall et al. 1998; Clark 2007). For our approach, probably fewer trees would suffice as only trees that survived or that did not experience a gap event were included. However, a larger sample size than presented here is probably required.

To obtain full insight in temporal patterns in forest dynamics, the complete disturbance history of the forest needs to be reconstructed. This entails inclusion of all trees of the dominant (canopy) tree species in a certain area to allow reconstruction of time of establishment, synchronization of the occurrence of releases in time, and the spatial scale of disturbances. In temperate forests, this approach is commonly applied (e.g. Lusk and Smith 1998; Rentch et al. 2003). For tropical forests, however, this approach may be somewhat far-fetched as these forests are more diverse and usually not all species form (reliable) annual growth rings (Baker et al. 2005; Brienen et al. 2009; but see Worbes et al. 2003). Still, such an approach can be applied for the species that do form reliable annual rings. When adjusting the techniques for the detection of releases and improving the sampling strategy, the reconstruction of release

frequencies over long time periods will help understanding long-term patterns of tropical forest dynamics.

Acknowledgments We are grateful to Mart Vlam for help with the ring measurements. We thank Nazareno Martínez, Miguel Cuadiay, Adhemar Saucedo, Jeroen Wiegeraad, Edwin Rodríguez, and many others for help with fieldwork. We are grateful to staff and personnel of PROMAB-UAB for logistic support. Logging company 'Maderera Boliviana Etienne S.A.' is acknowledged for permission to work in their concession and for logistic support. We thank Heinjo During for discussions on the data analysis and for providing constructive comments on an earlier version of the manuscript. DMAR was supported by grant W 84-608 from the Netherlands Organisation for Scientific Research (NWO).

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